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ORIGINAL PAPER

# Trait-mediated interaction leads to structural emergence in mutualistic networks

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**Abstract** As asymmetric structures of mutualistic networks can potentially contribute to system resilience, elucidating drivers behind the emergence of particular network architectures remains a major endeavour in ecology. Here, using an eco-evolutionary model for bipartite mutualistic networks with trait-mediated interactions, we explore how particular levels of connectance, nestedness and modularity are affected by three network assembly forces: resource accessibility, tolerance to trait difference between mutualistic pairs and competition intensity. We found that a moderate accessibility to intra-trophic resources and cross-trophic mutualistic support can result in a highly nested web, while low tolerance to trait difference between interacting pairs leads to a high level of modularity. Network-level trait complementarity leads to low connectance and high modularity, while network-level specialization can result in nested structures. Consequently, we argue that the interplay of ecological and evolutionary processes through trait-mediated interactions can explain these widely observed architectures in mutualistic networks.

**Keywords** Network architecture · Nestedness · Connectance · Compartmentalization · Modularity · Trait complementarity · Network specialization

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## Introduction

Mutualistic networks are formed by interactions between species who exploit each other for mutual benefit, such as the interactions between flowering plants and their pollinators and between many plants and their seed dispersers. Despite their diversity, mutualistic interactions exhibit surprisingly well-organized structures (Bascompte and Jordano 2007). In particular, they are often found to be within a certain range of connectance, nestedness and modularity (Bascompte and Jordano 2007; Jordano et al. 2003; Vazquèz and Aizen 2004). Connectance measures the proportion of realized interactions among all possible ones in a network, and mutualistic networks often have a low to moderate level of connectance (Olesen and Jordano 2002). A high level of nestedness, where specialists only interact with a subset of species with which generalists interact (Bascompte et al. 2003), is also a common feature of mutualistic networks (Thébault and Fontaine 2010). Modularity depicts the extent to which a network is compartmentalized into delimited modules where species are strongly interacting with species within the same module but not those from other modules (Olsen et al. 2007). Being a typical feature of food webs (Thébault and Fontaine 2010), high modularity is also common in some mutualistic networks (Olesen et al. 2007; Guimarães et al. 2007; Mello et al. 2011).

Probing mechanisms and processes that drive the emergence of these network structures is essential for safeguarding the ecosystem service provided by mutualistic networks, as network structures can have important roles in network stability and resilience (Bastolla et al. 2009; Thébault and Fontaine 2010). Some studies have hypothesized that network structures are the consequence of neutral processes such as random interactions between species, where the probability of an interaction depends only on the relative abundances of species (Vazquèz 2005; Stang et al. 2006; Vazquèz et al. 2007). In contrast, others have argued that these network structures are a consequence of non-neutral evolutionary and ecological processes (Olsen et al. 2007; Thompson et al. 2013; McQuaid and Britton 2013a; Encinas-Viso et al. 2014; Nuwagaba et al. 2015). For instance, phylogenetic history can partially explain the emergence of particular network structures (Rezende et al. 2007; Minoarivelo et al. 2014; Chamberlain et al. 2014), although the use of phylogeny developed from neutral genetic markers could mask the role of biotic interactions.

The concept of trait-mediated interaction has been a subject of much debate since its inception (Abrams 2007). Although it was originally defined to describe the indirect effect of a mediator species on the interaction between the two mediated species (Abrams et al. 1996), the term has gradually been adopted to describe any dependence of biotic interactions on traits (Bolker et al. 2003; Bolnick and Preisser 2005). While most studies on food webs still use its original meaning (Werner and Peacor 2003), studies on mutualistic interactions have preferred the broader meaning (Guimarães et al. 2011; Nuismer et al. 2010), which is the sense that will be employed in this study. Empirical and theoretical studies have shown that the adaptive response of behavioural and phenotypic traits to biotic interactions can swiftly alter the outcome of these interactions (Werner and Peacor 2003). For instance, differences in particular traits could constrain the possibility of interactions between species pairs, thus posing a threshold on traits for feasible interactions (Snow and Snow 1972; Bascompte et al. 2006; Stang et al. 2006). Such a threshold on traits has been found important for determining the interaction structures of many ecological networks (Stang et al. 2007). Trait-mediated interactions can be much stronger than density-mediated interactions (Wissinger and McGrady 1993; Railsback et al. 1999; Schmitz et al. 2004), especially in some pollination networks where the length distributions of proboscis

and floral tubes are better predictors of interaction incidence and strength than the relative abundances of species (Stang et al. 2009).

Although the effect of population density on biotic interactions is straightforward through the effected encounter rate, an increasing number of studies have resorted to the importance of behavioural and morphological traits in changing interaction strength and thus network structures. A number of studies have focused on the role of behavioural and morphological traits in shaping network structures (McQuaid and Britton 2013a; Chamberlain et al. 2014; Rafferty and Ives 2013). Biotic interactions could be directly mediated by a linkage rule between interacting traits (Santamaría and Gironés 2007), forming trait complementarity (high degree of trait matching between interacting pairs) and trait convergence (traits within a trophic tend to be more similar than expected) (Guimarães et al. 2011; Nuismer et al. 2012). Following on from these trait-based studies, we consider how interacting traits can potentially affect the emergence of network structures via mediating both the intra-trophic competition and the cross-trophic mutualistic interaction, with the interaction strength a function of the trait matching/difference between interacting species (Nuismer et al. 2010). The level of trait mismatching can be measured as the length difference between proboscis and pollen tube in a typical case of pollination syndrome, whilst as the size difference between the body/jaw and the fruit/seed in the case of frugivores and seed-dispersal networks.

In contrast to typical trait-based approaches, we design an eco-evolutionary model depicting simultaneously the ecological dynamics of population densities happening at a fast time scale and the evolutionary dynamics of interacting traits happening at a slow time scale, using the framework of *adaptive dynamics* (Metz et al. 1992; Dieckmann and Law 1996; Dercole and Rinaldi 2008). By analyzing the structures of resultant networks, we aim to investigate how features of trait-mediated interactions shape the architecture of mutualistic networks. In particular, we explore (1) how the specialization of trait-mediated interactions, including competition, mutualism and resource exploitation, affect the structures of mutualistic networks; (2) how much variation in network structures can be attributed to density-mediated interactions (measured by network size and total abundance) and trait-mediated interactions (measured by trait convergence and complementarity).

## Materials and methods

Evolutionary and ecological processes are intertwined. Evolutionary changes in functional traits can affect ecological processes such as the way species interact and subsequently the behaviour of population dynamics/demography. In return, functional traits will change in response to varying frequency-dependent selection from changing population densities. As such, we describe a model of mutualistic network emergence, implementing exactly such interdependence between population dynamics and trait evolution. Specifically, we assume that resource competition becomes intense between two species with similar traits. Moreover, matching traits between a pair of mutualistically interacting animal and plant species confers on them high fitness rewards. Following the framework of adaptive dynamics, traits can evolve disruptively and diversify adaptively into multiple interacting ones, forming an ecological network. Here we focus on how the specialty of trait-mediated interactions, i.e. the level of trait matching in resource competition and mutualistic interactions, affect the architecture of emerged mutualistic networks.

## Eco-evolutionary dynamics

Let there be $n$ functional morphs of animals and $m$ functional morphs of plants. Each functional morph, indexed by $i$ for animals and $j$ for plants, is characterized by its population density $A_i$ (for $i \in 1,\ldots, n$) and $P_j$ (for $j \in 1,\ldots, m$), respectively. We denote the trait of animal morph $i$ by $x_i$ and the trait of plant morph $j$ by $y_j$. The population dynamics of the system is depicted by a Lotka–Volterra model with a Holling (1959) type II functional response, as in Zhang et al. (2011) and Nuwagaba et al. (2015):

$$\frac{dA_i}{A_i dt} = f_A(x_i) = r_A - \frac{r_A \sum_k \gamma(x_i, x_k) A_k}{K_A(x_i)} + \frac{\sum_j b_{A_i P_j} w_{A_i P_j} P_j}{1 + h \sum_j w_{A_i P_j} P_j}, \tag{1a}$$

$$\frac{dP_j}{P_j dt} = f_P(y_j) = r_P - \frac{r_P \sum_k \gamma(y_j, y_k) P_k}{K_P(y_j)} + \frac{\sum_i b_{P_j A_i} w_{P_j A_i} A_i}{1 + h \sum_i w_{P_j A_i} A_i}, \tag{1b}$$

where $r$ is the intrinsic population growth rate, and $h$ the handling time that animals spend for visiting a plant and digesting the nutrients extracted from the plant; both are assumed to be trait-independent to avoid over-parameterization of the model ($r_A = r_P = 1$; $h = 0.1$). In the following, all terms in Eq. (1b) can be mirrored from the specified formulation in Eq. (1a).

The carrying capacity, $K_A$ and $K_P$, varies between morphs, representing trait-mediated resource accessibility. Following Doebeli and Dieckmann (2000), we used a Gaussian function for the carrying capacity: $K_A(x_i) = k_A N\left(x_A^{\max}, \sigma_A, x_i\right)$, where $k_A$ (=400) is a scaling constant, and $N\left(x_A^{\max}, \sigma_A, x_i\right)$ the Gaussian density function of trait $x_i$ with the maximum carrying capacity at $x_A^{\max}$ (=3) and the standard deviation $\sigma_A$. Similarly, we set the baseline values of $k_P$ (=300) and $y_P^{\max}$ (=2) for the plant species in the following analysis.

The intra-trophic competition function $\gamma$ is set to let morphs with more similar traits suffer stronger competition. We used a Gaussian function for depicting the competition intensity between morphs (Bürger et al. 2006; Doebeli and Dieckamann 2000; Doebeli and Ispolatov 2011; Raimundo et al. 2014): $\gamma(x_1, x_2) = \exp\left(-(x_1 - x_2)^2 / 2\sigma_C^2\right)$, where $\sigma_C$ controls the width of the competition kernel. The cross-trophic mutualistic benefit, $b_{AP}$, reflects the assumption of assortative interactions that matched traits bring to each other high profit, and is also assumed to follow a Gaussian function of trait difference: $b_{AP}\left(x_i, y_j\right) = c \cdot \exp\left(-\left(x_i - y_j\right)^2 / 2\sigma_m^2\right)$, where $c$ (=0.1) is a parameter controlling the magnitude of the maximum mutualistic support, and the parameter $\sigma_m$ controls the tolerance level of successful interactions to the dissimilarity of involved traits (Nuismer et al. 2010). The interaction preference of two morphs $w_{AP}$ determines the possibility of interaction after the encounter and is assumed to follow adaptive foraging strategies, depending on both the benefit and abundance of involved morphs (Doebeli and Dieckmann 2000; Zhang and Hui 2014). Modifying the expression which describes the strength of mutualistic support in Doebeli and Dieckmann (2000) and Egas et al. (2005), we have the following function for the adaptive interaction preference: $w_{A_i P_j} = b_{A_i P_j}^{\beta} \Sigma_k A_k / \Sigma_k \left(A_k b_{A_k P_j}\right)^{\beta}$, where $\beta$ is a parameter that determines whether the interaction is optimal ($\gg 1$), suboptimal (=1) or neutral (=0); the summation term $\Sigma_k A_k$ in the numerator is for normalization. For simplicity yet without losing generality, we chose $\beta = 1$ in the following analyses.

Functional traits of interacting morphs are subject to mutations. This can also be interpreted as the replacement and reassembling of local species through colonization and invasion of species with novel traits. Mutation normally happens at a low rate so that the populations can be considered at their ecological equilibriums when the mutation occurs (Doebeli and Dieckmann 2000). We only consider the non-trivial strictly positive and asymptotically stable equilibrium points of the system ($\tilde{A}_i(x_i, y_j)$ and $\tilde{P}_j(x_i, y_j)$). When a mutation enters the system, the resident morph and the mutant undergo an intra-trophic competition determined by Eq. (1). Let $x_i'$ and $y_j'$ be the mutant trait of animal morph $i$ and plant morph $j$, and let $X = (x_1,\ldots, x_n)$ and $Y = (y_1,\ldots, y_m)$ be the trait vectors of the resident morphs. We can define the invasion fitness of the rare mutants at the equilibrium points as their per-capita growth rates when setting their initial densities to be negligible: $f_A(x_i')$ and $f_P\left(y_j'\right)$. The selection gradient, defined as $g_{A_i} = \partial f_A(x_i')/\partial x_i'|_{x_i'=x_i}$ and $g_{P_j} = \partial f_P(y_j')/\partial y_j'|_{y_j'=y_j}$, determine the direction and speed of trait evolution, and an evolutionary singularity is defined as the traits $(\tilde{x}_i, \tilde{y}_j)$ when the selection gradient disappears. The evolutionary dynamics of the functional traits can be depicted by the canonical equations of adaptive dynamics (Dieckmann and Law 1996):

$$\begin{aligned} dx_i/dt &= m_A\tilde{A}_1 g_{A_i} \\ dy_j/dt &= m_P\tilde{P}_1 g_{P_j} \end{aligned}, \tag{2}$$

where $m_A$ and $m_P$ are parameters proportional to the rate and variation of the mutation (set to $10^{-3}$) in the analysis. An evolutionary branching is to occur in the system provided three conditions are satisfied. First, the singularity $(\tilde{x}_i, \tilde{y}_j)$ should be an evolutionary attractor of directional selection; that is, it is convergence stable. This happens when all eigenvalues of the Jacobian matrix of Eq. (2) have negative real parts (see Doebeli and Dieckmann 2000); this means $\partial g_{A_i}/\partial x_i|_{x_i=\tilde{x}_i} < 0$ and $\partial g_{P_j}/\partial y_j|_{y_j=\tilde{y}_j} < 0$. Second, the singularity should represent a fitness minimum to induce disruptive selection and to allow the mutant to invade (Geritz et al. 1998); that is, $\partial^2 f_A/\partial x_i'^2|_{x_i'=\tilde{x}_i} > 0$ and $\partial^2 f_P/\partial y_j'^2|_{y_j'=\tilde{y}_j} > 0$. Finally, the mutant and the resident morphs need to coexist to ensure the protection of dimorphism from the evolutionary branching (Geritz et al. 1998); that is, the two morphs can invade each other: $(\partial^2 f_A/\partial x_i^2 + \partial^2 f_A/\partial x_i'^2)|_{x_i'=x_i=\tilde{x}} > 0$ and $(\partial^2 f_P/\partial y_j^2 + \partial^2 f_P/\partial y_j'^2)|_{y_j'=y_j=\tilde{y}_j} > 0$.

## Numerical simulation

We numerically solved the population dynamics (Eq. 1) and the canonical equations of adaptive dynamics (Eq. 2), with an initial population density of 1 for both plants and animals (unless otherwise specified), and set the initial trait values to be different (2.25 for animals and 2.75 for plants). Note that, the dynamics of trait evolution is independent of the initial conditions as the system will converge to the same evolutionary singularity (Fig.S1). Following Doebeli and Dieckmann (2000), we only chose the aforementioned initial values for illustration, which can take any real numbers nonetheless. It is worth noting that, although the trait of a species can take any values (e.g. log-transformed body size as a focal trait can range from negative to positive infinity, theoretically speaking), only those that are feasible and can ensure its own viability, i.e. with a positive equilibrium in Eq. (1), can be realised in the model. Once the system reaches its singularity, the three conditions for evolutionary branching will be examined. If satisfied, a new morph will be

added to the system with its trait value slightly different from the resident trait (+0.01) and having a low initial density (10 % of its resident population density). The density of the resident morph will be simultaneously updated to be 90 % of its original. The process was repeated until the system reached its evolutionarily stable strategy (ESS). Not all observed ecological systems, as an ongoing evolving identity, have reached an ESS due to insufficient establishment duration and perturbations. For such cases where the system has an ESS but took too much computational time to reach some of its singularities, we stopped the simulation at $10^7$ evolutionary time steps. Note that there were cases where the system did not have an ESS (e.g. the case of Red Queen dynamics); we stopped the simulation after the system has reached its singularity repeatedly eight consecutive times.

We focused on the effects of three key parameters on the evolutionary dynamics, including the width of the intra-trophic competition kernel ($\sigma_C$), the tolerance to trait difference in a mutualistic interaction ($\sigma_m$) and the width of resources accessibility ($\sigma_A$ for animals and $\sigma_P$ for plants; we keep $\sigma_A = \sigma_P$ for simplicity). A wide competition kernel (large $\sigma_C$) indicates a low sensitivity of intra-specific competition to trait difference; that is, a species of such can compete with a wide range of species for resources. Low tolerance to trait difference (small $\sigma_m$) suggests that mutualistic benefits can only be assured by interacting with mutualistic partners with closely similar traits. Higher resource

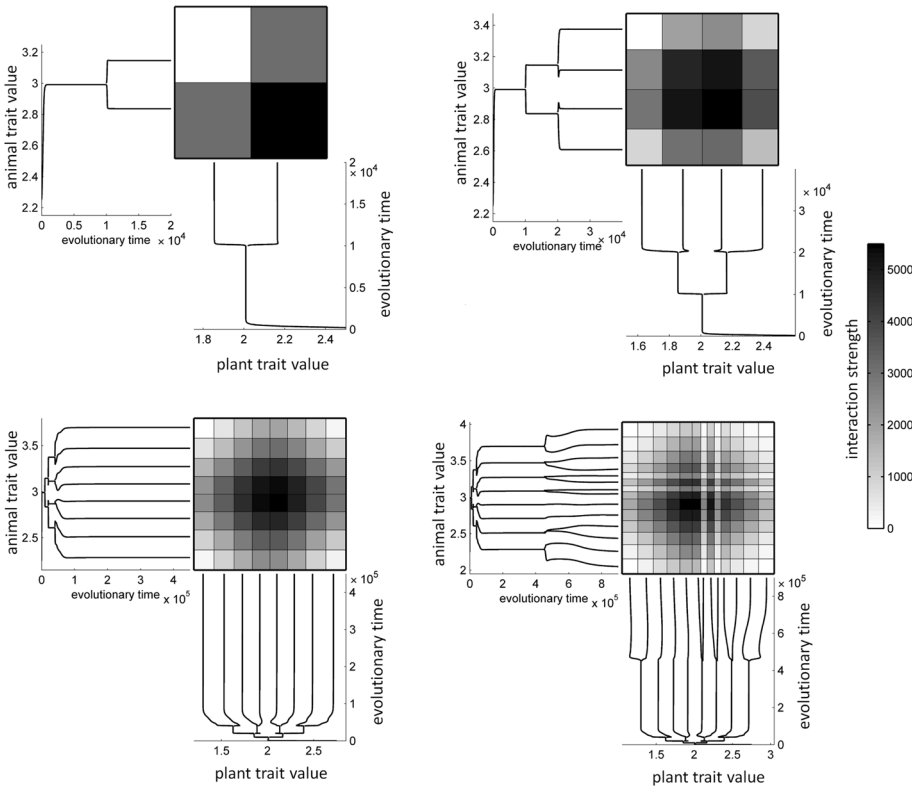


**Fig. 1** The evolutionary dynamics (four snapshots) of a bipartite mutualistic network, represented as the evolutionary trees of interacting traits and the interaction strength matrix. Parameters: $\sigma_A = e^{-1}$, $\sigma_c = e^{-2}$, $\sigma_m = e$

accessibility (large $\sigma_A$) indicates a wider exploitable niche space (Fig.S2). We simulated the evolutionary dynamics for all combinations of $\sigma_A$, $\sigma_C$ and $\sigma_m$, ranging from $e^{-3}$ ($\approx 0.05$) to $e$, with a multiplicative step of $e^{1/4}$; a total of 4913 ($=17^3$) runs. We ran additional parameter sensitivity tests on model behaviours, showing consistent and robust results (Fig.S3 and Fig.S4).

## Network analysis

We considered the bipartite mutualistic networks formed by interactions between the two sets of animal morphs and plant morphs produced at the end of each simulation. Cases where the system gave no evolutionary branching (monomorphic systems) were discarded from the study as they cannot be considered as a network. Although mutualistic interactions are typically recorded in a binary format, quantitative datasets can be more informative, especially with the potential of incorporating information on interaction strength (McQuaid and Britton 2013a; Schleuning et al. 2014). Here, we depicted the network as a quantitative interaction matrix ($Q$) where its elements ($q_{ij}$) represent the interaction strength between animal $i$ and plant $j$. Following Berlow et al. (2004), we define the interaction strength as the non-linear functional response term of Eq. (1), depending on both the number of recruited animals $i$ from interacting with animals $j$, and the number of recruited plants $j$ from interacting with animals $i$, per time unit:

$$q_{ij} = \frac{1}{2}\left(\frac{A_i b_{A_iP_j} w_{A_iP_j} P_j}{1 + h w_{A_iP_j} P_j} + \frac{P_j b_{P_jA_i} w_{P_jA_i} A_i}{1 + h w_{P_jA_i} A_i}\right). \quad (3)$$

When the element $q_{ij}$ is $<10^{-8}$, it was considered to be equal to zero, indicating a negligible interaction. An illustration of trait evolution in an ecological network, depicted as evolutionary trees and interaction matrices, is provided in Fig. 1.

We considered the following metrics for quantitative networks. First, the quantitative connectance metric was computed as the quantitative linkage density divided by the number of species in the network (Tylianakis et al. 2007). Second, we used the metric WNODF (Weighted Nestedness metric based on Overlap and Decreasing fill) for depicting the level of nestedness (Almeida-Neto and Ulrich 2011). Finally, the level of modularity was measured using a new algorithm *QuanBimo* (Dormann and Strauβ 2014; adapted from Claused et al. 2008). All these network metric measurements are implemented in the R library *bipartite* (Dormann et al. 2008).

To further investigate the possible causes of network structure, a few additional network-level metrics were computed. First, the level of specialization of each network was measured according to the quantitative index $H_2'$ of Blüthgen et al. (2006), implemented in the R library *bipartite* (Dormann et al. 2008). This index measures the overall deviation of species' realized degrees from their expected ones, ranging from 0 (no specialization) to 1 (perfect specialization). Second, to quantify the level of trait divergence in each trophic (animal or plant), we used the functional trait dispersion index *FDis* (Laliberté and Legendre 2010). It depicts the mean distance of individual species trait to the centroid of all species traits, weighted by population abundance of each species, ranging from 0 (no dispersion) to 1 (highly dispersed), implemented in the R library *FD* (Laliberté et al. 2014). Third, we measured the trait complementarity between animals and plants after modifying Guimarães et al.'s (Guimarães et al. 2011) metric to incorporate the effect of interaction strength, $Cp = -\ln D$, where $D = (\Sigma_i \Sigma_j D_{ij})/(n \times m)$ is the average phenotypic trait

difference between interacting pairs, weighted by the normalized interaction strength, $D_{ij} = |x_i - y_j| \times \bar{q}_{ij}$. Finally, network size ($N$) was measured as the total number of animal and plant morphs at the end of the simulation.

We tested the effect of network size ($N$), total abundance ($Ab$), level of trait complementarity ($Cp$), animal and plant functional trait dispersion ($FDis_{an}$ *and* $FDis_{pl}$) on network structures (connectance, nestedness and modularity) using a linear regression. Before the linear regression, we assessed the mutlicollinearity of these explanatory variables using the variance inflation factor (VIF), implemented in the R library *fmsb* (Nakazawa 2014). The variable with the highest VIF score was first removed, and then a new VIF analysis was performed until all the VIF scores of the remaining variables were below five. These selected variables were then used in the linear regression. We estimated the contribution of a particular variable to explaining the variation of network structures as the reduction of adjusted $R^2$ after removing the variable.

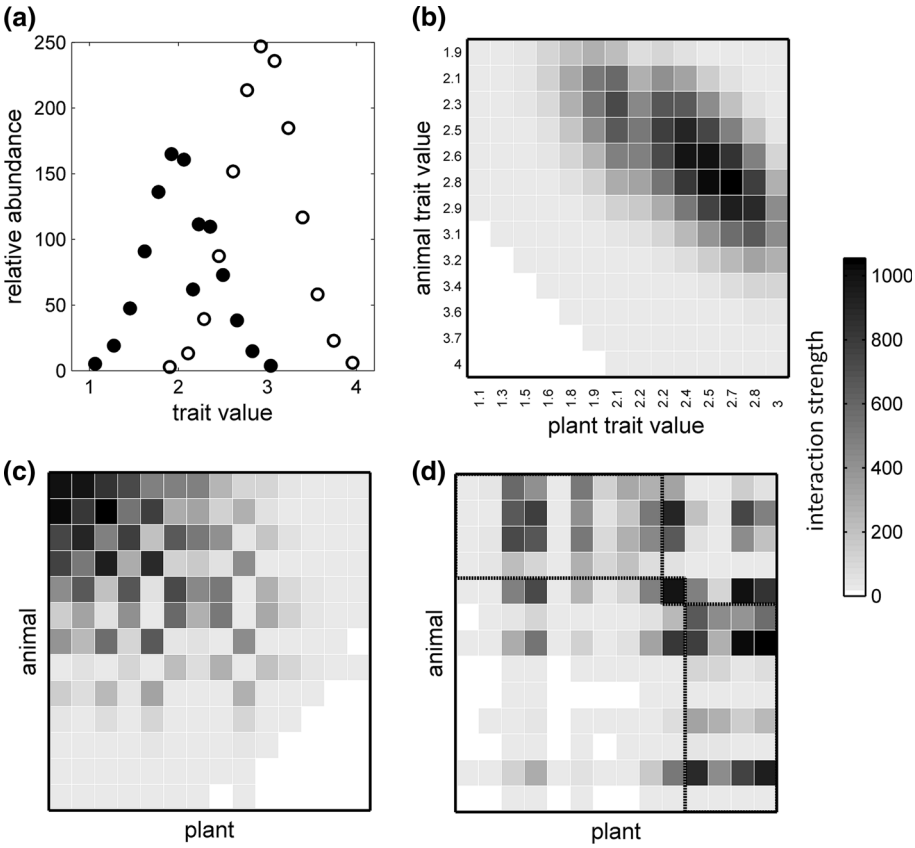


**Fig. 2** An example of a mutualistic network produced from the model. **a** Relationships between trait values and their corresponding population abundance of animals (*open circles*) and plants (*closed circles*). **b** The weighted matrix of interaction strength, with *rows* and *columns* sorted according to trait values. **c** *Rows* and *columns* are sorted to show the pattern of nestedness (WNODF = 0.58). **d** *Rows* and *columns* are sorted to show the pattern of modularity (Mod = 0.23). Parameters: $\sigma_A = e^{-1}$, $\sigma_c = e^{-2}$, $\sigma_m = e^{-1}$

## Results

### Network structure emergence

The model can produce mutualistic networks with structures comparable to real networks (see Fig. 2 for an illustration of patterns on relative abundance and interaction matrices sorted for traits, nestedness and modularity). For all tested parameter values, connectance ranged from 0.015 to 0.5 with an average of 0.26 ± 0.14 (mean ± standard deviation; in the same format hereafter), with highly connected networks emerging when the resource accessibility is narrow (small $\sigma_A$) and the tolerance to trait difference is high (large $\sigma_m$) but insensitive to the change of intra-trophic competition kernel ($\sigma_C$) (Fig. 3 first column). Nestedness ranged from 0 (no pattern of nestedness) to 1 (perfectly nested), with an

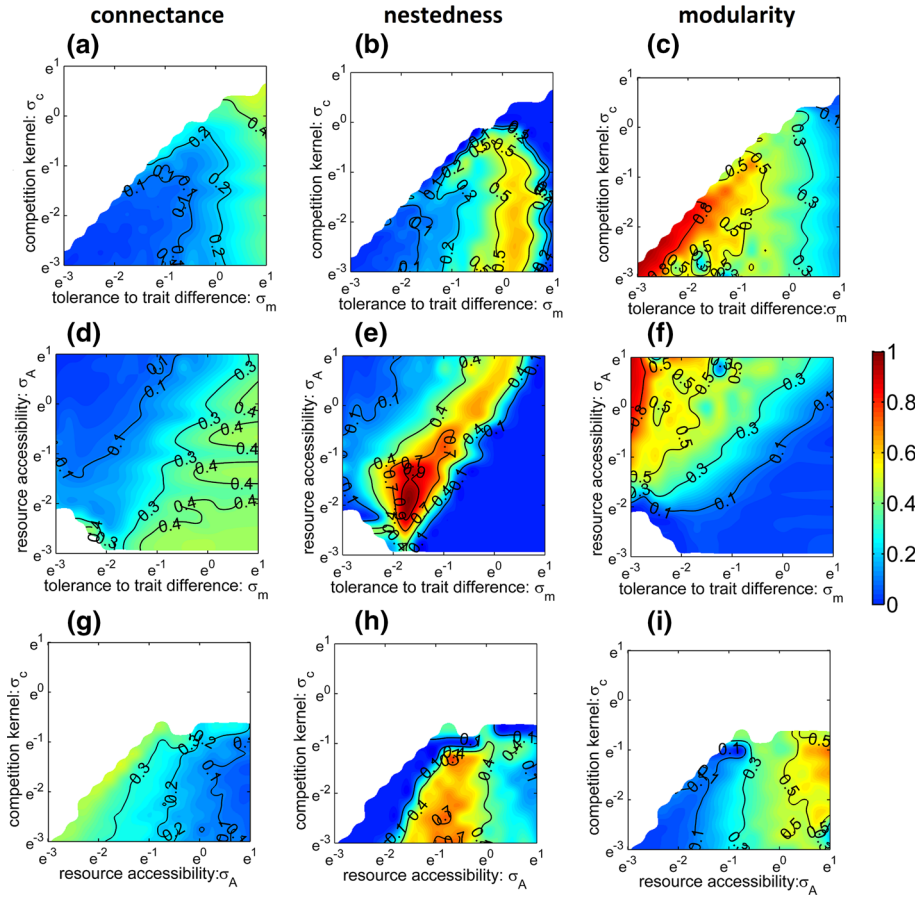


**Fig. 3** The quantitative connectance (*first column*), weighted nestedness (*second column*) and quantitative modularity (*third column*) of emerged networks as a function of model parameters ($\sigma_A$, $\sigma_c$ and $\sigma_m$). Specifically, in each plot we varied two parameters and kept the third parameter fixed. The fixed parameters are $\sigma_A = e^{0.75}$ for the *first row*, $\sigma_c = e^{-3}$ for the *second row*, and $\sigma_m = e^{-1}$ for the *third row*, respectively. The *white* area in each plot represents unfeasible parameter zone where the system becomes monomorphic with no network metrics calculated

average of 0.22 ± 0.25; highly nested networks emerged when the resource accessibility ($\sigma_A$) and the tolerance to trait difference ($\sigma_m$) were moderate but with a narrow competition kernel (small $\sigma_C$) (Fig. 3 second column). Modularity ranged from 0 (no signal of compartmentalization) to 0.96 (highly compartmentalized networks) with an average of 0.28 ± 0.22, with highly compartmentalized networks emerging when the resource accessibility is high (large $\sigma_A$), the intra-trophic competition kernel low or moderate ($\sigma_C$), and the tolerance to trait difference low (small $\sigma_m$) (Fig. 3 third column). Model parameters and metrics for all simulated networks were given in Table S1.

As the level of nestedness is, by definition, related to how generalists and specialists interact with each other, we further examined the specialization level $\left(H_2'\right)$ of each network. The level of specialization increased slightly with increase in the intra-trophic resource accessibility ($\sigma_A$) but decreased notably with increase in tolerance to trait difference ($\sigma_m$) (see the color patterns of Fig. 4). High resource accessibility made cross-trophic interaction redundant and thus reduced the potential of the emergence of highly structured networks (Fig. 4a). Low tolerance to trait difference facilitated reciprocal specialization and broke down nested structures (Fig. 4b). In contrast, generalists prevailed when the tolerance to trait difference is high, thus also breaking down the highly nested structures (Fig. 4b). Only a moderate level of specialization can foster high nestedness, which can be achieved through a moderate level of resource accessibility and tolerance to trait difference.

## Network variation explained

Two variables were removed from the linear regression based on the VIF analysis: animal functional trait dispersion ($FDis_{an}$) and total abundance ($Ab$). $FDis_{pl}$ was found to be strongly positively correlated with plant trait dispersion, while ($Ab$) was positively correlated with network size (Fig.S5). All three remaining explanatory variables ($N$, $Cp$,

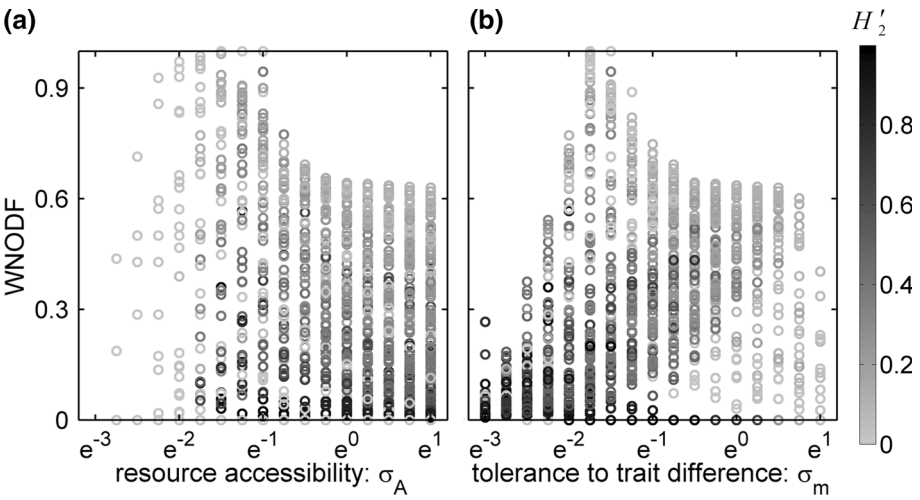


**Fig. 4** Weighted nestedness degree of the simulated networks with respect to resource accessibility and the tolerance to trait difference. The *gray* level of each point, representing one network, is the level of specialization ($H_2'$ index). See Table S1 for details

$FDis_{pl}$) had a significant effect on network structure, except for the trait dispersion on connectance (Table 1). A large portion of variation of connectance (83 %) and modularity (72 %) were explained, although only 11 % variation of nestedness was explained by these three variables.

The explained variation of network connectance dropped drastically when trait complementarity ($Cp$) was removed from the linear regression (Table 1), suggesting it to be the most important constraint to high connectance (Fig. 5). Trait dispersion ($FDis_{pl}$) and network size ($N$) contributed trivially to the variation of network connectance (Table 1). The small percentage of nestedness variation explained (11 %) was mostly due to the contribution of trait complementarity and trait dispersion (Table 1). Network modularity was mostly affected by trait complementarity, followed by trait dispersion, with the contribution from network size negligible (Table 1), suggesting that an increase in trait complementarity and trait dispersion could enhance network compartmentalization (Fig. 5). Modules were largely formed by species with similar traits (due to trait complementarity); however, species with asymmetric traits can also form modules, especially when trait dispersion was driving the emergence of compartmentalization (Fig.S6). The connectance, nestedness and modularity of simulated networks formed an interesting hook shaped relationship in the 3-dimentional space (Fig. 6).

## Discussion

By allowing both population density and interacting traits to change, we have made the mutualistic network adaptive at the network assemblage level. The model generated networks comparable to those reported in literature. Our estimates of quantitative connectance ($0.26 \pm 0.14$) are higher than those observed empirically from qualitative networks with binary interaction strength matrices, with a mean of 0.11 in Olesen and Jordano (2002), $0.18 \pm 0.15$ in Rezende et al. (2007). The connectance decreases with network size following a power law (Fig.S7), consistent with the result from Rezende et al. (2007) (see also the appendix in Suweis et al. 2013). Our average estimate of nestedness ($0.22 \pm 0.25$) is lower than the one from empirical networks ($0.37 \pm 0.18$; Rezende et al. 2007; Minoarivelo et al. 2014). Such discrepancies could be due to that we used interaction

**Table 1** Linear regression of connectance, nestedness and modularity on network size ($N$), trait complementarity ($Cp$) and plant trait functional dispersion ($FDis_{pl}$)

| | Connectance | Nestedness | Modularity |
|---|---|---|---|
| $N$ | −0.032 | 0.035 | $-2.56 \times 10^{-4}$ |
| $Cp$ | −0.116 | 0.066 | 0.073 |
| $Fdis_{pl}$ | −0.001 $^{ns}$ | −0.059 | 0.667 |
| Full model | 0.83 | 0.11 | 0.72 |
| $Cp + FDis_{pl}$ | 0.77 | 0.09 | 0.71 |
| $N + FDis_{pl}$ | 0.19 | 0.04 | 0.32 |
| $N + Cp$ | 0.82 | 0.05 | 0.63 |

The first horizontal panel shows the regression coefficients for each variable (*ns* non-significant; all the rest are significant with $p < 0.001$); the second panel shows the adjusted $R^2$ for the full model and reduced models (after removing one variable)

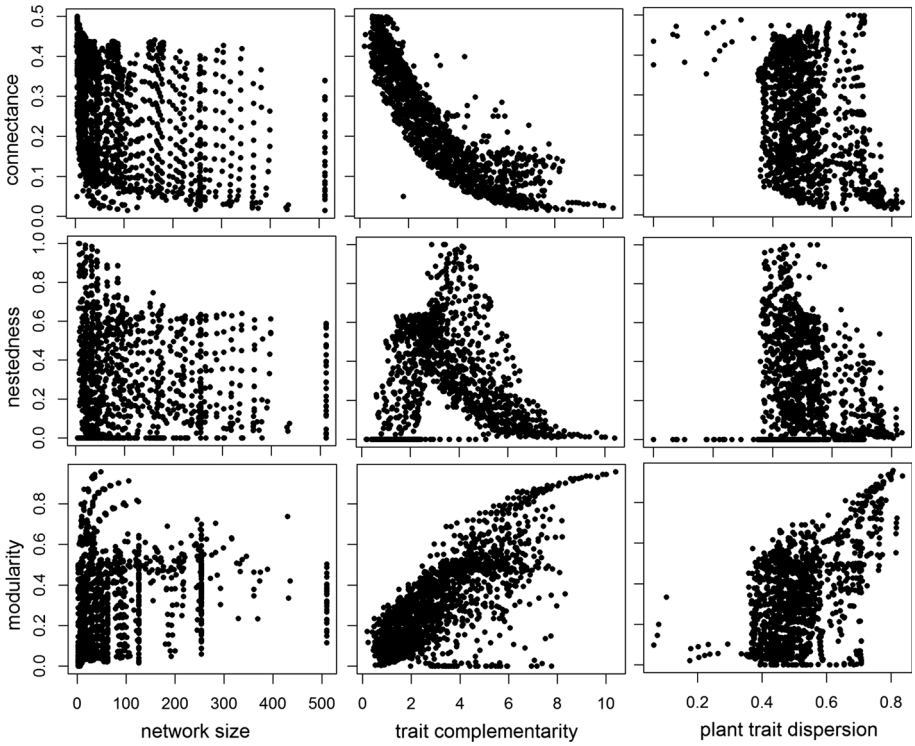


**Fig. 5** Relationships between network structures (connectance, nestedness and modularity) and explanatory variables (network size, trait complementarity, plant trait dispersion). See Table S1 for details

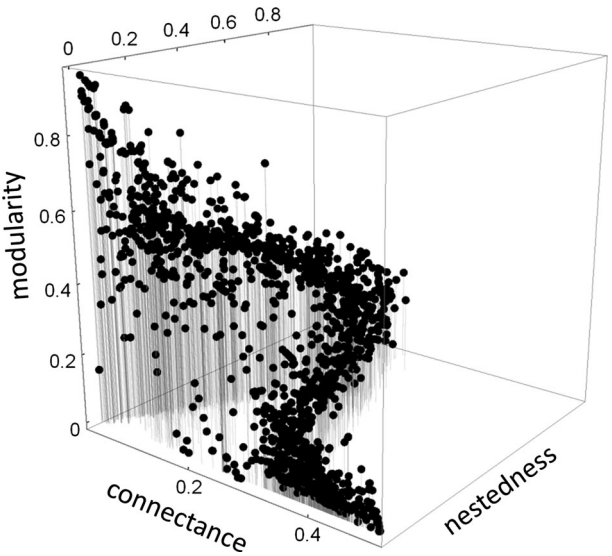


**Fig. 6** Relationships between connectance, nestedness and modularity for simulated networks. See Table S1 for details

strength matrices, rather than binary incidence matrices as used in the mentioned literature. As such, our matrices are less likely to contain zero entries, with many networks fully connected. Networks with no zero entries are automatically scored zero for nestedness, potentially skewed our estimates of connectance and nestedness. In contrast, as algorithms for estimating modularity are designed for considering weighted networks (Schelling and Hui 2015), the estimates of modularity ($0.28 \pm 0.22$) fit well with the observed ones from empirical mutualistic networks ($0.27 \pm 0.09$; Rezende et al. 2007; Minoarivelo et al. 2014).

Nuismer et al. (2012) have suggested that trait-mediated interaction could lead to anti-nested structures in networks due to strong reciprocal specialization. This happens in our system when the tolerance to trait difference ($\sigma_m$) is low as species become selective when choosing their mutualistic partners, leading to a high level of specialization and thus a low level of nestedness (Fig. 3). However, when mutualistic benefit ($b_{AP}$) and resource exploitation ($K_A$ and $K_P$) contribute comparably to the fitness, the network could become highly nested; this can be achieved at a moderate level of interaction specialization. Adding to McQuaid and Britton's (2013a) conclusion that nested networks can emerge from trait evolution under trade-offs on exploiting mutualistic benefits, we here further showed that the accessibility to both the mutualistic benefit (i.e., the tolerance to trait difference $\sigma_m$) and the intra-trophic resources ($\sigma_A$) can affect the way species interact and thus shape nested structures.

Empirical mutualistic networks can be highly compartmentalized (Guimarães et al. 2007; Olsen et al. 2007; Donatti et al. 2011; Mello et al. 2011); this happens in our system when the intra-trophic resource accessibility ($\sigma_A$) is high and the tolerance to trait difference ($\sigma_m$) is low. Parameters for high modularity are not compatible with those for high nestedness, consistent with the result from Fortuna et al. (2010), showing a changing sign of correlation between nestedness and modularity when changing the level of connectance (Fig. 6). Moreover, our finding that interaction modules are largely formed by species with similar traits (Fig.S6) is consistent with the conclusion of Fort and Mungan (2015) on a Mediterranean plant–pollinator network (Stang et al. 2007). By classifying pairs of plants and pollinators into modules based on matching their traits, Fort and Mungan (2015) were able to accurately predict plant and pollinator abundances. As modularity was best explained by trait complementarity (Table 1), drivers of trait complementarity, arising either through coevolution (Olesen et al. 2007; Rezende et al. 2007; Minoarivelo et al. 2014) or adaptive rewiring (Zhang et al. 2011; Schleuning et al. 2014; Nuwagaba et al. 2015), could play crucial roles in the process of network compartmentalization (Donatti et al. 2011; Chamberlain et al. 2014).

Cross-trophic exploitation of resources and mutualistic benefits affected network structures, while intra-trophic competition had a trivial effect on the emergence of asymmetric network structures. This could be because cross-trophic interactions directly affect interaction strength (Eq. 3), while intra-trophic competition only indirectly affects interaction strength through its influence on population size. To this end, competition might not be a driver of the emergence of asymmetric network structures (Bastolla et al. 2009; Encinas-Viso et al. 2012), but only a force of community assembly process.

Trait-mediated direct interactions are apparent in our system (mutualistic interactions and intra-trophic competition), while trait-mediated indirect interactions do also exist here (Peacor and Werner 1997). Indeed, a species can indirectly affect the competition strength between its mutualistic partners. The two mediated species face a trade-off during trait evolution, between targeting mutualistic benefit and resource accessibility, similar to a well-studied model depicting two predators competing for one prey (Werner and Peacor

2003; Mowles et al. 2011). Phenotypic adaptation of the mediator species induced by one predator can either hamper or improve the foraging efficiency of the other predator (Werner and Peacor 2003). In our case, the mediator species changes its trait to become more similar to its mutualistic partners for maximizing mutualistic benefit. However, if the intra-specific competition kernel ($\sigma_C$) is large, two competing species tend to diverge their traits to avoid competition, and the trait of the mediator species will follow the trait of one mutualistic partner. The effectiveness of the other competitor is diminished as a result. However, when $\sigma_C$ is small, traits of the two competing species are close to each other. Both species can thus explore the mutualistic benefits, and consequently mutualism is facilitated. As a narrow intra-specific kernel ($\sigma_C$) corresponds to a high level of nestedness (the case for many empirical mutualistic networks), our study confirms that mutualistic interactions can be a facilitator to competition (Bastolla et al. 2009).

Certainly, using a specific trait to build potential networks could over-simplify the reality. Empirical studies usually make use of a number of functional and behavioral traits judged to be important in structuring the networks (Chamberlain et al. 2010, 2014; Donatti et al. 2011). However, using a single trait to construct potential interaction networks could be simplistic as species with mismatched traits can be part of the same module (Fig.S6). Proposing a multi-dimensional trait space could bring more realism to trait-based network analysis.

Although we here only investigated the structural emergence of mutualistic networks, the model can be opted for antagonistic networks and food webs. Some studies have already appreciated the importance of the linkage between ecological and evolutionary processes for understanding the emergence of complex but realistic food webs (Loeuille and Loreau 2005; Ito and Ikegami 2006; Brännströms et al. 2011). However, the eco-evolutionary approach of network emergence is rarely used for studying antagonistic networks and would certainly deserve more attention. In particular, the host-parasite network model by McQuaid and Britton (2013b) can be considered a good start along this research direction, showing the emergence of nestedness from the evolution of trait-mediated interactions. The appreciation of eco-evolutionary feedbacks in methods of adaptive dynamics and other continuous-trait evolutionary game theory could help to unveil the role of evolutionary processes in the formation of community assemblages and ecological networks (Hui et al. 2015), which are considered in the mainstream through only environmental filtering and biotic interactions.

We assumed that all the morphs are the results of diversification and evolved together under the same environmental conditions (Rezende et al. 2007; Minoarivelo et al. 2014). This contrasts the studies which emphasize the roles of environmental forces, species invasion/colonization and adaptive species rewiring in network emergence (Zhang et al. 2011; Nuwagaba et al. 2015). The fact that a combination of ecological and evolutionary factors explained poorly the nestedness pattern may reveal that some network assemblages can be strongly influenced by external environmental factors such as climate variability (Dalsgaard et al. 2013; Hui et al. 2013; Boyero et al. 2015; Welti and Joern 2015), rather than population demography and life-history traits. On this note, future trait-based network models could encompass these other forces that effect network assemblies (Stouffer et al. 2014; Campbell et al. 2015).

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